

## MIMICRY OF ANTS OF THE GENUS *ZACRYPTOCERUS* (HYMENOPTERA: FORMICIDAE)

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*Abstract.*—Within the myrmicine ant genus *Zacryptocerus* 13 of 21 species in Central America are hypothesized to be models for a Batesian mimicry complex that includes at least 40 species of arthropods. The ants are striking in appearance because they are strongly flattened and silvery in color, and use chemical defenses against potential predators, although they are eaten by ant specialists and as reproductives. The ants nest and forage arboreally and most of the identified mimics used dead branches in some way. The larger number of mimetic species than models appears possible because of the abundance of the ants and the relative rarity of the mimics; the rarity is further enhanced by the host specificity of most of the mimics, supporting a model proposed by Brower. Mimics appear to become absolutely and relatively more numerous toward the equator. The selective agents (“operators”) are thought to be generalist insectivorous birds; ant specialists are argued not to affect evolution of the system.

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Collection of beetles of the genus *Agrilus* (Buprestidae) in southern Central America and their subsequent study in museum collections (Hespenheide, 1974, 1979, and unpublished) has revealed a set of species from different species groups that possess a common pattern of color and pubescence. Members of other families of beetles, Hymenoptera, Heteroptera, and spiders with similar patterns were also discovered through field collections, museum study, and review of the literature. The beetles appear to be ant mimics with a specific type of model. Ants are involved in mimicry complexes with other insects and spiders in at least three different ways ecologically (Edmunds, 1974; Reiskind, 1977; Rettenmeyer, 1970): 1) as typical Batesian models for less well defended mimetic forms; 2) as models for insects which live as commensals with the ants (Wasmannian mimicry); or 3) as models for spider predators of ants (Peckhamian mimicry).

The rather large number of distinctively patterned species involved in this mimetic complex recommend the present study, which is also intended to raise some additional questions, both about ant mimicry and about mimicry in general. My collections and experience with both models and mimics have been restricted to Central America and most comments will concern species which occur there, although the system occurs and likely is as much or more complex in South America.

### THE MODELS

The ant models were easily identified as belonging to the myrmicine genus *Zacryptocerus* (sensu lato, Kempf, 1973; includes species referred to in earlier literature as *Cryptocerus* and *Paracryptocerus*) of the tribe Cephalotini. The Cephalotini are known as models of mimetic spiders (Reiskind and Levi, 1967). Nevermann (1930) independently pointed out the resemblance of his *Ethelema costaricensis* (Colydiidae)

to *Zacryptocerus multispinosus biguttatus* (Emery) (under the synonym "*Cryptocerus gibbosus* Fr. Smith"; Kempf, 1972), Vogt (1949) mentioned the resemblance of *Agrilus ornatulus* Horn to *Zacryptocerus texanus* (Santschi), and Ekis (1976) noted the similarity of his *Enoclerus canus* (Cleridae) to *Zacryptocerus cristatus* (Emery).

The tribe Cephalotini consists of four genera containing about 113 species of ants (Kempf, 1972), of which 3 genera and 30 species occur in Central America. This paper will consider only the genus *Zacryptocerus*, although the genera *Cephalotes* is (Reiskind, pers. comm.) and *Procryptocerus* may be involved in mimicry complexes of their own. *Zacryptocerus* includes 21 species and one additional subspecies in Central America, all of which belong to the group of species previously placed in *Paracryptocerus* (Kempf, 1972; Snelling, unpublished); three species reach the United States (Smith, 1947), and 49 additional species are known from South America.

*Zacryptocerus* species have worker, soldier and reproductive castes, of which only the workers are considered in detail in this paper. *Zacryptocerus* workers of a given species are relatively uniform in size and coloration. Species tend to fall into one of three or four groups based on visually distinct facies; of these, the one including the largest number of species serves as a model for the mimetic forms described here. Species of this group are characterized by a strongly flattened and broad body form and head, and by an integument that is predominantly black but that is more or less densely covered with white scales which give an overall silvery-grey appearance (Fig. 1). Among the 21 Central American species, three (the "*wheeleri* group," Snelling, 1968; Fig. 2) are narrower, lack the conspicuous scales, do not therefore look very conspicuously different from other black ants, and seem to lack mimics (see discussion below). A fourth species *Z. umbraculatus* (Fig. 3) is predominantly red in coloration and has a darker gaster distinctly marked with yellow; it may be involved in other mimicry complexes, but will not be considered further here. Of the 17 remaining species, three are poorly known (*Z. basalis*, *bimaculatus*, and *sobrius*) and one is often predominantly reddish (*Z. pallens*), so that the following discussion will focus on 13 species which likely serve as models: *Z. aztecus* (Forel), *christophersoni* (Forel), *cristatus*, *curvistriatus* (Forel), *foliaceus* (Emery), *maculatus* (Fr. Smith), *minutus* (F.), *multispinus* (Emery), *multispinosus* (Norton), *porrasi* (Wheeler), *scutulatus* (Fr. Smith), *setulifer* (Emery), and *texanus*.

#### WHY MIMIC *Zacryptocerus*?

Of the three types of ant mimicry, only Batesian mimicry is an option for *Agrilus* and most of the other mimics discussed here, in that the mimetic species usually feed on wood and not inquilines or predators on ants. The distinctive appearance of *Zacryptocerus* is not itself sufficient basis for the convergent (or divergent—see Brower and Brower, 1972) evolution of mimetic forms—i.e., as a model for a Batesian mimicry complex—there must also be some basis for avoidance of the ant model by a somewhat generalized insectivorous predator potentially common to both the ant and any would-be mimic. Edmunds (1974), Reiskind (1977), and Rettenmeyer (1970) have pointed out that ants are often models for Batesian mimicry complexes because of any or all of three characteristics dissuasive to predators: 1) poisonous stings; 2) biting mouthparts, in some cases accompanied by chemical irritants; and/or 3) distastefulness, sometimes associated with pheromone systems. The primary defense of

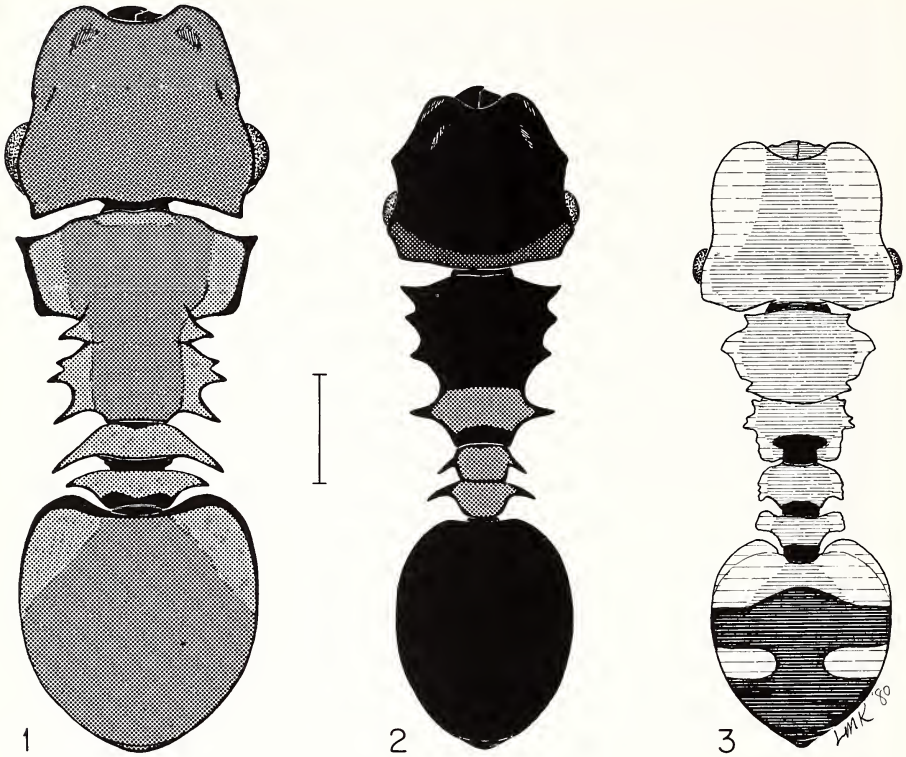


Fig. 1-3. Species of *Zacryptocerus*. 1. *Z. cristatus*. 2. *Z. rohweri*. 3. *Z. umbraculatus*— only *Z. cristatus* serves as a model for the mimicry complex described here. Scale indicates 1 mm.

*Zacryptocerus* seems to consist in distastefulness; they do not seem to have a sting of any consequence (unlike the predatory Ponerinae or the aggressive *Pseudomyrmex*; Janzen, 1966), and their mandibles are relatively small (Coyle, 1965). Coyle (1966) has studied the defensive behavior of three species of *Zacryptocerus* (*multispinosus biguttatus*, *multispinus*, and *umbraculatus*) in Costa Rica and found that, other than freezing or moving away, all three used chemicals released from the gaster or oral region as their primary defense. Workers picked up by me in the field for collection or examination typically have a very strong odor. In *Z. multispinus* an additional defensive maneuver consists of curling up into a ball so as to expose spines on the lateral margins of the thorax and petiolar segments. These defenses are not successful against all insectivorous birds: a specimen of the woodcreeper *Dendrocolaptes souleyetii* collected in Costa Rica by D. R. Paulson had consumed 9 *Zacryptocerus* workers and soldiers of two species (*multispinosus biguttatus* and *umbraculatus*) among 61 ants and 67 total prey (see discussion below). T. W. Sherry (1984) found small numbers of reproductive *Zacryptocerus* taken by several species of Tyrannidae in lowland Costa Rica, but this is not relevant to a mimicry system based on worker models.

ECOLOGY OF *Zacryptocerus*

*Zacryptocerus* is an arboreal ant that is characteristic of wet tropical forests, but also occurs into the subtropics as far north as the southwestern United States and extreme southern Florida (Smith, 1947). Members of the genus exhibit strongly dimorphic worker and soldier castes, and the latter are textbook examples (e.g., Wilson, 1971: 160f; also Creighton, 1963) of the highly specialized phragmotic defense of the nest. The biology of these ants has been studied in some detail for two species found in the United States, *Z. texanus* (Creighton and Gregg, 1954; Creighton, 1963) and *Z. rohweri* (Creighton and Nutting, 1965), and for several Costa Rican species (Coyle, 1965 and unpublished). Additionally, Wheeler (1942) lists a number of nest site records for members of the genus. Adults regularly forage on leaves or, more frequently, run on trunks and branches. In mature forests colonies are primarily in the canopy (Coyle, 1965), as evidenced by their being observed in numbers on recent tree falls or blowdowns. Colonies may be divided among a number of nests (Coyle, 1965; Creighton, 1963) and are commonly in dead branches. Creighton (1963) and Creighton and Nutting (1965) record nests of *Z. texanus* and *Z. rohweri* in the old larval burrows of smaller wood-boring beetles, including the Buprestidae, and the distinctive shape of the emergence hole figured (Creighton, 1963) for one nest suggests that it is a burrow of *Agrilus* (see below). Probably because of the defensive rather than aggressive nature of these ants, no species have been identified as obligate plant-ants (in the sense of Janzen, 1966), although Janzen (1974) records the genus as one of five using the swollen-thorn *Acacia ruddiae* Janzen, an atypical forest species which lacks a consistent association with *Pseudomyrmex*, and Wheeler (1942) reports nests in other ant-plants. As arboreal ants *Zacryptocerus* are peripheral participants in other ant-plant mutualistic systems: Wheeler (1910) reports Muller's observation of *Zacryptocerus* species visiting bead glands of *Bunchosia*; and *Zacryptocerus* spp. visit extrafloral nectaries of *Bixa orellana* L. (Bentley 1977), *Ipomea carnea* (Keeler 1978), and *Byttneria aculeata* (Hespenheide, 1985a). Jeanne (1979) reports *Z. multispinus* at baits of wasp brood in Costa Rica and an undetermined *Zacryptocerus* at similar baits in Pará, Brazil. Overall, the microhabitat of *Zacryptocerus* seems to be primarily that of dead branches (the most common nest sites), secondarily that of living branches (for nest sites or trails), and finally of leaf surfaces (for solitary workers foraging, especially for pollen, nectar, and/or honeydew—Creighton, 1963; Creighton and Nutting, 1965).

## MIMETIC INSECTS AND SPIDERS

*Agrilus* (Buprestidae)

As noted above, Vogt (1949) first pointed out the resemblance of a species of *Agrilus* to one of *Zacryptocerus*. Collection and study of species of *Agrilus* occurring or likely to occur in the region from Mexico through Panama have revealed 22 species of *Agrilus* that are marked in such a way that they resemble *Zacryptocerus* species. A number of other *Agrilus* are patterned in ways that resemble ants other than *Zacryptocerus*. The dorsal aspect of model species of *Zacryptocerus* (Fig. 1) is visually dominated by the broad head and gaster, both silvery-grey in overall appearance. Putative mimetic *Agrilus* (Fig. 4) typically combine the following characteristics: (1)

the head and pronotum shining black and more or less densely invested with white pubescence which yields an overall silvery appearance; (b) the anterior halves of the elytra deep matte black with a more or less complicated pubescent design of two or three transverse, oblique, and/or longitudinal bars; and (c) the posterior halves of the elytra again abruptly and densely pubescent, in some species then becoming sparser toward the apex. The overall effect is then a tripartite silvery/variegated/silvery, which corresponds to head/pronotum-and-petiole/gaster of the ants. Although a complete systematic study of the more than 600 species of Central American *Agrilus* remains to be made, it is clear that the mimetic forms belong to a number of different species groups within the genus and have therefore evolved independently. Table 1 lists the names of the described species considered to be mimetic, as well as the names of other insects and spiders in the complex. In addition to the Central American species, at least 7 South American *Agrilus* appear to mimic *Zacryptocerus*, including *A. dolatus* Kerremans and *A. esculentis* Fisher.

Only *Agrilus* among the Buprestidae has been identified with *Zacryptocerus*-like patterns, despite the similarity of ecology among most genera in the family (other than the leaf-mining forms). Absence of mimicry in other genera is likely due to their being either proportionately broader or larger overall than these rather small ants. Even among *Agrilus*, those 22 species which are mimetic of *Zacryptocerus* average significantly smaller in size than all 607 species recognized in the fauna (4.90 mm vs. 6.45 mm;  $P_t < 0.001$ ).

Most *Agrilus* species are narrowly host-specific cambium miners in recently dead or dying wood (Fisher, 1928). Host range is typically a single plant species or several species within the same genus, rarely more than one genus (fewer than 10% of the species). Adults are found on branches of the host, especially those favorable as oviposition sites, or feeding on the leaves of the host, or, more rarely, on leaves or branches of plants near hosts. The size of adult *Agrilus* is related to the size of the branches mined by the larvae; i.e., smaller *Agrilus* bore smaller branches (Hespenheide, 1976).

#### Other Mimics

Field collections and study of the Biologia Centrali-Americana collection in the British Museum of Natural History has shown that a number of other groups of insects share the silvery/variegated/silvery pattern of *Agrilus* (Table 1, Fig. 5–9). Additional species in these and other families (e.g., Melasidae and Mordellidae) were not included in this discussion because they lack the precision of the pattern of those included—most frequently the middle region is alternatively simply black rather than variegated—although it seems likely that in some cases the resemblance would be effectively mimetic. The ecology of these other mimics is discussed briefly as follows:

*Coleoptera*. Anthribidae: This family as a group is commonly collected at tree falls where the larvae are presumably involved in feeding on fungi.

Bruchidae: Members of this family are seed predators (Janzen, 1969).

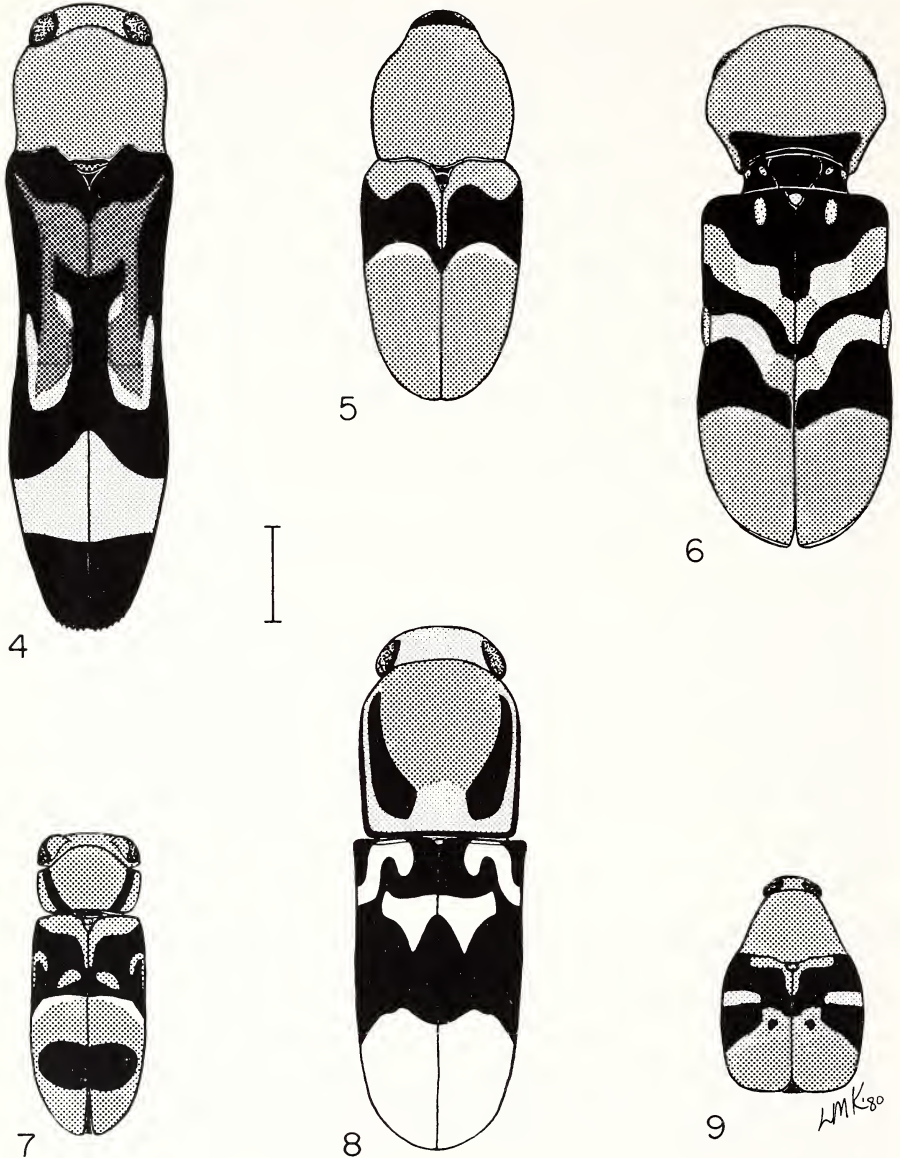
Cerambycidae: This family is infrequently involved in this complex probably for the same reason as are larger Buprestidae as well as because of their nocturnal activity periods. Chemsak and Linsley (1978) guessed that *Pseudotapnia* was an ant mimic from its unusual morphology. South American Cerambycidae in the British Museum

Table 1. Arthropods mimetic of *Zacryptocerus* ants in Central America.

Taxon	# spp.	Names of described species
Coleoptera		
Anthribidae		
<i>Eugonops</i>	1	<i>championi</i> Jordan
<i>Eugonus</i>	1	<i>decorus</i> Jordan
Bruchidae		
<i>Acanthoscelides</i>	1	<i>suaveolus</i> Sharp
Buprestidae		
<i>Agrilus</i>	22	<i>blandulus</i> Guerin, <i>buscki</i> Fisher, <i>lautellus</i> Fisher, <i>ornatus</i> Horn, <i>signatus</i> Waterhouse, <i>tezcattipocai</i> Fisher, <i>titlaceabanae</i> Fisher
Cerambycidae		
<i>Pseudotapnia</i>	1	<i>curticornis</i> Chemsak & Linsley
Cleridae		
<i>Enoclerus</i>	2	<i>canus</i> Ekis, <i>cinereus</i> Gorham
<i>Phyllobaenus</i>	3	
Colydiidae		
<i>Ethelema</i>	2	<i>decorata</i> Sharp, <i>costaricensis</i> Nevermann
Curculionidae-Baridinae		
<i>Coelonertus</i>	1	<i>nigrirostris</i> Solari
Curculionidae-Zygopinae		
<i>Eulechriops</i>	1	<i>cylindricollis</i> Champion
<i>Helleriella</i>	1	<i>ruddiae</i> Hespenheide
<i>Cylindrocopturinus</i>	1	<i>hainesi</i> Hespenheide
Hymenoptera		
Orussidae		
<i>Ophrella</i>	1	<i>lingulata</i> Middlekauff
Heteroptera		
Lygaeidae		
<i>Neocattarus</i>	1	
Araneae		
Salticidae		
Undet.	1	

that seem to be part of this complex include species under the following names there: *Aemylos triangulifer* Auriv., *Argyronides pulchella* Bates, *Epropetes cleroides* White, *Parazodes erythrocephalus*.

Cleridae: Clerids as larvae are predaceous on wood-boring beetles and are often found running on fallen trees. Interestingly, the genus *Epiphloeus* has not been found by me with a *Zacryptocerus* pattern, although it is an appropriate size, has rather complicated pubescent patterns, and is involved in other mimicry complexes (Hespenheide, 1973). Adult behavior differs significantly from *Enoclerus* and *Phyllobaenus*, however, in that adults are usually found sitting motionless on the vertical sides or undersides of branches, rather than running actively.



Figs. 4-9. Mimetic species of beetles. 4. *Agrilus ornatulus* (Buprestidae). 5. *Coelonertus nigrirostris* (Curculionidae, subf. Baridinae). 6. *Enoclerus cinereus* (Cleridae). 7. *Ethelema decorata* (Colydiidae); 8. *Eugonus decorus* (Anthribidae). 9. *Acanthoscelides sauveolus* (Bruchidae). Scale indicates 1 mm.

Colydiidae: As noted above, Nevermann (1930) noted the resemblance of his species *Ethelema costaricensis* to *Zacryptocerus*. He mentions collecting both insects on fallen trees and considers the possibility *Ethelema* is an inquiline of *Zacryptocerus* and thereby a Wassmannian mimic, but he concedes he has never seen a beetle associated with a nest of the ants and discusses the difficulty of finding such an association. Nevermann also mentions, however, that *Ethelema* was collected on logs already attacked by (a) species of Scolytidae. I have also collected colydiids in association with scolytids and/or platypodids, and it seems more likely to me the beetles are predators of these other wood-boring beetles.

Curculionidae: Most weevils of the subfamily Zygopinae are wood-borers, and I would guess that to be true of *Eulechriops cylindricollis* Champion and *Cylindrocopturinus*, although less certainly for the latter because its morphology is unusual in other details than overall appearance (Hespenheide, 1985b). On the other hand, *Helleriella ruddiae* is especially interesting because of its ecological association with *Acacia ruddiae* (Hespenheide, 1980; Janzen, 1974, see above) and, thereby, with *Zacryptocerus*. Specimens of *Helleriella ruddiae* were reared by Janzen from swollen thorns of the *Acacia* unoccupied by ants, as are other *Helleriella*. Other swollen-thorn *Helleriella* are somewhat ant-like in appearance, typically with reddish or blackish areas set off by narrow bands of white scales. It is especially interesting that in a species of *Acacia* that lacks *Pseudomyrmex*, the associated *Helleriella* has evolved a color pattern that is similar to that of one of the other ants that replaces *Pseudomyrmex*, albeit on a less regular basis. Other Zygopinae from Central America (*Lechriops albovariegata* and *canescens* Champion) and South America (*Mnemyne viduata* Pascoe, *Copturus mimetica* Hespenheide) suggest *Zacryptocerus* but differ in small details from the pattern narrowly-defined above.

Hymenoptera. Orussidae: Members of this family are typically parasitoids of wood-boring beetles, especially the Buprestidae.

Hemiptera-Heteroptera. Lygaeidae: Specimens of one species of *Neocattarus* were collected on leaves of bushes under a fruiting fig (*Ficus* sp.) where these bugs were feeding on fallen seeds (Slater, 1972). I have seen *Ficus* both at the Smithsonian Tropical Research Institute's Ancon headquarters and Barro Colorado Island station with colonies of several species of *Zacryptocerus*. Although I know of no reason for a consistent association of *Zacryptocerus* with *Ficus*, it appears to have been frequent enough for evolution of resemblance by the bug to the ant to have been to the advantage of the former. Although many of the *Neocattarus* were collected on the ground where most of the fruits were fallen, numbers of adults were also searching the leaves of bushes, presumably for seeds defecated by feeding birds. *Zacryptocerus* seems never to forage on the ground (Creighton, 1963), so that the advantage of the mimicry may accrue only to the smaller part of the population on aboveground vegetation, since the putative predators (see below) also forage off the ground.

#### QUESTIONS RAISED BY THE MIMICRY OF *Zacryptocerus*

##### Community Ecology of *Zacryptocerus* Mimics

The ecological unity of this complex centers on the use of dead branches. The model *Zacryptocerus* spp. nest in such branches. Of the 40 mimetic species listed in Table 1 and discussed above, 26 are wood-borers (including the ant-*Acacia* inhabitant



*Helleriella*), 8 are predators or parasitoids of wood-borers, 2 feed on fungi of dead wood, the spider is a solitary predator collected on a tree trunk, and 3 are seed predators or of unknown ecology. Of the 11 South American species known to me, all are wood-borers.

In the absence of evidence that any of the 40 species of mimics are themselves distasteful, they are all assumed to be Batesian mimics of the 13 widespread model species of *Zacryptocerus*. This imbalance in overall numbers of models and mimics raises the question of a differential in the relative population sizes of these groups as required of a Batesian mimicry relationship. Jackson and Drummond (1974) report four arthropod Batesian mimics of the arboreal ant *Camponotus planatus* in Belize, but found that the ant models comprised about 30% of individual arthropods collected from vegetation, whereas the four mimics comprised only 2% of the same samples. They also note that four species is the largest number of mimics reported for a single ant model. No attempt has been made here to associate particular mimic species with particular species of *Zacryptocerus*—although it might be partially possible on the basis of relative sizes—but the overall complex is certainly much larger than that for the *Camponotus*.

Although the number of mimetic species is greater than the number of model species, the abundance of *Zacryptocerus* worker individuals is certainly much higher than the cumulative abundance of their mimics in all habitats. Published colony sizes for *Zacryptocerus* range from as few as 27 (for *Z. texanus*; Creighton and Gregg, 1954) to as high as 752 (polydomous colony of *Z. multispinus*; Coyle, 1965), with as many as 694 for a single nest (Coyle, 1965). The related *Cephalotes atratus* occurs in colonies of more than 10,000 (Weber, 1957). Few of the mimetic species, on the other hand, are known from more than a half-dozen specimens from all museums combined, although under very favorable conditions they may be relatively numerous locally on a host plant (G. H. Nelson has collected a few dozen *Agrilus ornatulus* on its host *Sapindus*, and the *Neocattarus* were relatively abundant under the single *Ficus* tree during the brief fruiting period characteristic of species of the genus).

*Zacryptocerus* species are, of course, not specific to particular plant species, although they may favor certain species or genera; Creighton and Gregg (1954) report most *Z. texanus* nests from the live oaks *Quercus virginiana* and *Q. fusiformis*, and neotropical *Zacryptocerus* may favor *Ficus* (see above; also *Acacia ruddiae*) without being restricted to them.

The general ecological-demographic pattern of this mimicry complex therefore seems to be the following: A small number of model species range widely over the many plant species in the community and are locally numerous at nests of a few 10's or 100's of individuals. The mimics are primarily host-specific wood-boring or fungus-feeding beetles which are low in numbers, usually solitary, and restricted to the vicinity of their particular plant hosts. A smaller number of less numerous parasitoids and predators may range more widely. The larger number of mimetic species does not endanger the model-mimic ratio required of Batesian systems because of their regular dispersion over the community as a consequence of their host specific plant preferences. Interestingly, this pattern of distribution of mimics was predicted by Brower (1958) as a consequence of the ability of visually-hunting predators to form search images. Brower proposed his model in terms of closely-related and therefore



Fig. 10. Zones in Central America for biogeographical analysis (Table 2). Lines follow national or state (Mexico) boundaries. Zone 2 includes only states bordering on Mexico.

morphologically similar procryptic insects, which is analogous to convergently-similar Batesian mimics, and both share the primary requirement of narrow host plant specificity. Much of the theory and most examples of mimicry derive from free-flying and therefore relatively widely-ranging Lepidoptera. In the system described here, and in many other systems encountered in my study of *Agrius* and ecologically related organisms, the more restricted mobility of the participating species (in this case especially of the models) allows a "structure" that almost certainly permits greater complexity to the system.

#### Biogeography of the Mimicry Complex

A variety of studies of marine (Bakus and Green, 1974; Palmer, 1979; Vermeij, 1978) and terrestrial organisms (Connell, 1970; Janzen, 1970; Elton, 1973), has produced evidence that suggests the intensity of predation increases toward the trop-

Table 2. Geographic distribution of *Zacryptocerus* models and *Agrilus* (Buprestidae) and other insect mimics.

Zone <sup>1</sup>	Ants	Total spp.	Mimics		
			<i>Agrilus</i> mimics (% fauna)	Others	Total
2	1	109	2 (0.8)	0	2
3	2	74	1 (1.4)	0	1
4	4	146	0	0	0
5	5	171	2 (1.2)	0	2
6	5	205	9 (4.4)	2	11
7	8	90	2 (2.2)	3	5
8	8	44	1 (2.3)	4	5
9	10	38	1 (2.6)	4	5
10	9	64	3 (4.6)	8	11
11	9	70	8 (11.4)	9	17
Total	17	607	22 (3.6)	15	37

<sup>1</sup> See Figure 10 for delimitation of geographic zones.

ics. One may divide Central America and the immediately adjacent portion of the United States into 11 geopolitical zones that are roughly cross sections of the Central American isthmus (Fig. 10). One may then compare the distributions of the 13 more common putative model species of *Zacryptocerus* (Kempf, 1972; Snelling, unpublished) with those of the mimetic species (various taxonomic studies, Hespeneide, unpubl.). The results of this comparison are presented in Table 2. The number of ants increase toward South America and so, in general, do the numbers of mimetic species.

The genus *Agrilus* accounts for the largest number of mimetic species but does not as a genus overall increase regularly in numbers of species toward the equator but, rather, peaks in Mexico and then declines. However, if one divides the number of mimetic *Agrilus* in each zone by the total number of *Agrilus* species in that zone (Table 2), the proportion of mimetic forms does increase more regularly. This might be taken as evidence of higher predation intensity as one moves toward the tropics, except that the increase in the proportion of species mimetic of *Zacryptocerus* is accompanied by both increases and decreases in the proportions of mimetic species involved in complexes with other models (e.g., Hespeneide, 1973, 1975a). The overall pattern is complex, but the highest proportions of mimetic species of all types are highest at the southeastern end of the geographical gradient and therefore consistent with the observations that marine invertebrates are more heavily defended in more tropical areas (Palmer, 1979; Vermeij, 1978).

There is a definite collection bias among non-*Agrilus* mimics to those areas I have collected (Costa Rica, Panama), so that the larger absolute numbers of mimics there cannot be taken as evidence for higher predation rates selecting for more sophisticated antipredator adaptations. The proportions of mimetic *Agrilus* are free of such a bias, in that non-mimetic species are collected as vigorously as mimics.

One interesting result of the biogeographic analysis is the difference in the presence

of mimetic *Agrilus* up the eastern and western coasts of Mexico. On the east coast, *Z. texanus* has two *Agrilus* mimics (*lautuellus*, *ornatulus*) as far north as Texas. On the west coast, only the "wheeleri" group of *Zacryptocerus* is found north of Nayarit, and no mimetic *Agrilus* has been found to date north or west of the Federal District. This observation bears out the exclusion of that section of the genus from the complex and from the present discussion (see above) on the basis of its less distinctive morphology.

#### Relative Importance of Specialized vs. Generalized Insectivores

Turner's (1977) succinct question—"Who are the dupes?" (the "operator" in Vane-Wright's, 1976, classification of mimetic relationships)—is appropriate in view of the observations above that *Zacryptocerus* are fed on by some birds. Sherry (1984) found that flycatchers in lowland Costa Rica fed on reproductives, but reproductive ants in mating flights are widely eaten by birds (Thiollay, 1970) and are essentially unprotected compared to workers. The evidence from the single *Lepidocolaptes* stomach mentioned above suggests that species is a specialist on non-reproductive ants, and the presence of a soldier caste member suggests the bird fed on a nest rather than on solitary workers. As a forest-based, arboreal forager, *Lepidocolaptes* should take *Zacryptocerus* regularly. Woodpeckers other than *Colaptes* (see above, also Hespdenheide, 1975b; Kilham, 1979), anteaters (Lubin et al., 1977), and lizards (Schoener, 1966) are also arboreally foraging specialists on ants, but also certainly constitute a minority among insectivorous organisms.

That some insectivores specialize on ants does not invalidate ant mimicry and would actually have little effect on the evolution of mimicry, apart from selecting for greater defenses by the ant models, since the mimicry would only be effective on generalist insectivores that would avoid distasteful (to them) ants in favor of other taxa. Looking like an ant might increase the risk of a mimic to an ant-eating specialist such as *Lepidocolaptes*, except that such specialists usually search out nests and colonies rather than solitary workers (Kilham, 1979). The relative importance of generalist insectivores *contra* specialists in the evolution of mimicry is thus analogous to the responses of herbivores to the evolution of plant chemical defenses: generalists are deterred whereas specialists are not (Rhoades and Cates, 1976).

Generalist insectivores which have the potential for encountering the greatest numbers of models and mimics in the habitat of both (see above) would be those foraging on branches and twigs. In Central America these would include primarily woodpeckers (Picidae), woodcreepers (Dendrocolaptidae), certain overbirds (Furnariidae, such as *Xenops*, *Premnoplex*, *Margarornis*), and the migrant black-and-white warbler (*Mniotilta*) among birds; *Anolis* and geckos among lizards; and certain tree-running mantids and reduviid bugs. The importance of vision likely restricts the important predators to the birds and lizards, and the readiness of at least some *Anolis* to eat ants (Schoener, 1966) may limit the number of appropriate lizards. Both the woodpeckers and wood-creepers include generalist as well as ant-specialist species (Cruz and Johnson, 1979; Hespdenheide, 1975b, and unpublished) and, in terms of both numbers of species and relative abundance are probably the most important selective agents in the evolution of this mimicry complex, with the role of lizards being uncertain.

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## LITERATURE CITED

- Bakus, G. J. and G. Green. 1974. Toxicity in sponges and holothurians: a geographic pattern. *Science* 185:951-953.
- Bentley, B. L. 1977. The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* (Bixaceae). *J. Ecol.* 65:27-38.
- Brower, L. P. 1958. Bird predation and food plant specificity in closely related procrystic insects. *Amer. Natur.* 92:183-187.
- Brower, L. P. and J. V. Z. Brower. 1972. Parallelism, convergence, divergence and the new concept of advergence in the evolution of mimicry. *Trans. Conn. Acad. Arts Sci.* 44: 59-67.
- Chemsak, J. A. and E. G. Linsley. 1978. New Neotropical Lamiinae (Coleoptera: Cerambycidae). *Pan-Pacific Entomol.* 54:26-30.
- Connell, J. H. 1970. On the role of natural enemies in preventing competitive exclusion in some marine animals and rain forest trees. *Proc. Adv. Study Dynamics Numbers Popul.*, pp. 298-312.
- Coyle, F. A. 1965. Preliminary observations on the ecology and behavior of Costa Rican cephalotine ants. Course Research Report, Organization for Tropical Studies Course, Biology and Evolution of Tropical Insects, pp. 45-65.
- Coyle, F. A. 1966. Defensive behavior and associated morphological features in three species of the ant genus *Paracryptocerus*. *Insectes Sociaux* 13:93-104.
- Creighton, W. S. 1963. Further studies on the habits of *Cryptocerus texanus* Santschi (Hymenoptera: Formicidae). *Psyche* 70:133-143.
- Creighton, W. S. and R. E. Gregg. 1954. Studies on the habits and distribution of *Cryptocerus texanus* Santschi (Hymenoptera: Formicidae). *Psyche* 61:41-57.
- Creighton, W. S. and W. L. Nutting. 1965. The habits and distribution of *Cryptocerus rohweri* Wheeler (Hymenoptera: Formicidae). *Psyche* 72:59-64.
- Cruz, A. and D. W. Johnston. 1979. Occurrence and feeding ecology of the common flicker on Grand Cayman Island. *Condor* 81:370-375.
- Edmunds, M. 1974. *Defence in Animals: A Survey of Anti-predator Defences*. Longman, Burnt Mill, Essex, England, xvii + 357 pp.
- Ekis, G. 1976. Neotropical checkered beetles of the genus *Enoclerus* (Coleoptera: Cleridae: Clerinae) *Beitr. Neotrop. Fauna* 11:151-172.
- Elton, C. S. 1973. The structure of invertebrate populations inside Neotropical rain forest. *J. Anim. Ecol.* 42:55-104.

- Fisher, W. S. 1928. A revision of the North American species of buprestid beetles belonging to the genus *Agrilus*. U.S. Natl. Mus. Bull. 145:1-347.
- Hespenheide, H. A. 1973. A novel mimicry complex: beetles and flies. J. Entomol. (London), A, 48:49-56.
- Hespenheide, H. A. 1974. Nomenclatural notes on the Agrilinae (Coleoptera, Buprestidae): II. *Agrilus*. Entomol. News 85:48-53.
- Hespenheide, H. A. 1975a. Reversed sex-limited mimicry in a beetle. Evolution 29:780-783.
- Hespenheide, H. A. 1975b. Prey characteristics and predator niche width. Pages 158-180 in: M. L. Cody and J. M. Diamond (eds.), Ecology and Evolution of Communities, Harvard Univ. Press, Cambridge, Massachusetts.
- Hespenheide, H. A. 1976. Patterns in the use of single plant hosts by wood-boring beetles. Oikos 27:161-164.
- Hespenheide, H. A. 1979. Nomenclatural notes on the Agrilinae (Buprestidae): IV. Coleop. Bull. 33:105-123.
- Hespenheide, H. A. 1980. New species and a review of the genus *Helleriella* (Coleoptera, Curculionidae, Zygopinae). Coleop. Bull. 34:323-332.
- Hespenheide, H. A. 1985a. The visitor fauna of extrafloral nectaries of *Byttneria aculeata* (Sterculiaceae): Relative importance and roles. Ecol. Entomol. 10:191-204.
- Hespenheide, H. A. 1985b. New Neotropical species of putative ant-mimicking weevils (Curculionidae: Zygopinae). Coleop. Bull. 38:313-321.
- Jackson, J. F. and B. A. Drummond. 1974. A Batesian ant-mimicry complex from the mountain pine ridge of British Honduras, with an example of transformational mimicry. Amer. Midl. Natur. 91:248-251.
- Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. Evolution 20:249-275.
- Janzen, D. H. 1969. Seed eaters versus seed size, number, toxicity and dispersal. Evolution 23:1-27.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. Amer. Natur. 104:501-528.
- Janzen, D. H. 1974. Swollen-thorn acacias of Central America. Smithsonian Contr. Bot. 13: 1-131.
- Jeanne, R. L. 1979. A latitudinal gradient in rates of ant predation. Ecology 60:1211-1224.
- Keeler, K. H. 1978. Insects feeding at extrafloral nectaries of *Ipomoea carnea* (Convolvulaceae). Entomol. News 89:163-168.
- Kempf, W. W. 1972. Catalogo abreviado das formigas da regio Neotropical (Hymenoptera: Formicidae). Studia Entomol. 15:3-344.
- Kempf, W. W. 1973. A new *Zacryptocerus* from Brasil, with remarks on the generic classification of the tribe Cephalotini (Hymenoptera, Formicidae). Studia Entomologica 16: 449-462.
- Kilham, L. 1979. Chestnut-colored woodpeckers feeding as a pair on ants. Wilson Bull. 91: 149-150.
- Lubin, Y. D., G. G. Montgomery and O. P. Young. 1977. Food resources of anteaters (Edentata: Myrmecophagidae) I. A year's census of arboreal nests of ants and termites on Barro Colorado Island, Panama Canal Zone. Biotropica 9:26-34.
- Middlekauff, W. W. 1985. *Ophrella*, a new genus of Orussidae from Panama (Hymenoptera: Symphyta, Orussidae). Pan-Pacific Entomologist 61:184-186.
- Nevermann, F. 1930. Zwei neue Colydiiden aus Costa Rica (Col.). Entomol. Blat. 26:110-114.
- Palmer, A. R. 1979. Fish predation and the evolution of gastropod shell structure: experimental and geographic evidence. Evolution 33:697-713.

- Reiskind, J. 1977. Ant-mimicry in Panamanian clubionid and salticid spiders (Araneae: Clubionidae, Salticidae). *Biotropica* 9:1-8.
- Reiskind, J. and H. W. Levi. 1967. *Anatea*, an ant mimicking Theridiid spider from New Caledonia (Araneae: Theridiidae). *Psyche*, Camb. 74:20-23.
- Rettenmeyer, C. W. 1970. Insect mimicry. *Annu. Rev. Entomol.* 15:43-74.
- Rhoades, D. F. and R. G. Cates. 1976. Toward a general theory of plant antiherbivore chemistry. *Recent Adv. Phytochem.* 10:168-213.
- Schoener, T. W. 1966. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155:474-477.
- Sherry, T. W. 1984. Comparative dietary ecology of sympatric, insectivorous neotropical flycatchers (Tyrannidae). *Ecological Monographs* 54:313-338.
- Silberglied, R. E. and A. Aiello. 1976. Defensive adaptations of some Neotropical long-horned beetles (Coleoptera: Cerambycidae): antennal spines, tergiversation, and double mimicry. *Psyche* 83:256-262.
- Slater, J. A. 1972. Lygaeid bugs (Hemiptera: Lygaeidae) as seed predators of figs. *Biotropica* 4:145-151.
- Smith, M. R. 1947. Ants of the genus *Cryptocerus* F., in the United States. *Proc. Entomol. Soc. Washington* 49:29-40.
- Snelling, R. R. 1968. Taxonomic notes on Mexican cephalotine ants (Hymenoptera: Formicidae). *Los Angeles Co. Mus. Contr. Sci.* 132:1-10.
- Thiollay, J.-M. 1970. L'exploitation par les oiseaux des essaimges de fourmis et termites dans une zone de contact savane-foret en Côte d'Ivoire. *Alauda* 38:255-273.
- Turner, J. R. G. 1977. Butterfly mimicry: the genetical evolution of an adaptation. *Evolutionary Biol.* 10:163-206.
- Vane-Wright, R. I. 1976. A unified classification of mimetic resemblances. *Biol. J. Linnean Soc.* 8:25-56.
- Vermeij, G. J. 1978. *Biogeography and Adaptation, Patterns of Marine Life*. Harvard Univ. Press, Cambridge, Massachusetts, xiii + 332 pp.
- Vogt, G. B. 1949. A biologically annotated list of the Buprestidae of the lower Rio Grande Valley, Texas. *Ann. Ent. Soc. Am.* 42:191-202.
- Weber, N. A. 1957. The nest of an anomalous colony of the arboreal ant *Cephalotes atratus*. *Psyche* 64:60-69.
- Wheeler, W. M. 1910. *Ants: Their Structure, Development, and Behavior*. Columbia Univ. Press, New York, xxv + 663 pp.
- Wheeler, W. M. 1942. Studies of Neotropical ant-plants and their ants. *Bull. Mus. Comp. Zool.*, Harvard 90:1-262, plates 1-57.
- Wilson, E. O. 1971. *The Insect Societies*. Harvard Univ. Press, Cambridge, Massachusetts, x + 548 pp.

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